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CONSERVATION IMPACT OF CLIMATIC VARIABILITY ON POLLINATION OF THE FEDERALLY ENDANGERED PLANT, *CLEMATIS SOCIALIS* (RANUNCULACEAE)

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ABSTRACT - Biotic pollination should be an important consideration when devising management plans for endangered plant species. In this study we documented inter-annual shifts in the suite of floral visitors to *Clematis socialis*, a federally endangered species. These pollinator shifts were correlated with shifts in climatic variables that we used as a proxy for the potential effects of climatic change. In addition, we characterized floral visitor behavior and conducted single-visit seed set experiments to assess the pollination effectiveness of floral visitors. Five insect species visited flowers of *C. socialis*: two lepidopteran species (*Erynnis juvenalis* and *Hemaris diffinis*) and three bee species (*Anthophora ursina*, *Bombus pennsylvanicus* and *Xylocopa virginica*). Due to their relatively greater frequency of flower visitation and high single-visit seed set (ca. 2.6–3 seeds/visit), two bee species (*Anthophora ursina* and *Bombus pennsylvanicus*) are considered to be the major pollinators of *C. socialis*. However, the relative importance of each pollinator species varied between years. *Anthophora ursina* was the most important pollinator in 1997, a year when *C. socialis* bloomed later in the spring. Queens of *Bombus pennsylvanicus* were the primary pollinator during 1996, a year when *C. socialis* bloomed relatively early in the spring. We conclude that management plans that focus on the "best pollinator" of a suite of pollinators may not preserve the long-term reproductive integrity of endangered plants with generalized pollination systems. We further conclude that asynchrony between flowering season and pollinator activity patterns may be a risk factor associated with human-caused global climate change.

INTRODUCTION

The Earth's biota is currently experiencing a major, human-caused, extinction event (Wilson 2002). Recent assessments estimate that worldwide 22–47% of flowering plants worldwide (Pitman and Jørgensen 2002) and more than 33% of flowering plant species in the United States are vulnerable to extinction (Stein and Flack 1997). Until recently, plant conservation efforts often focused on protecting populations without considering protection for the community-level processes

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that maintain these populations (Meffe and Carroll 1997). Many authors (Boyd 1994; Buchmann and Nabhan 1996; Johnson 1992; Kearns et al. 1998; Lesica 1993; Robertson et al. 1998; Spira 2001; Timmerman-Erskine and Boyd 1999) have suggested that interspecific interactions that benefit endangered plants (including pollination) must be maintained in order to ensure the long-term survival of these plant species. Unfortunately, the mutualists (pollination and otherwise) of many endangered plants are not known (Nabhan 1996). Even when pollinators are known, often little information is available regarding their habitat requirements, behaviors and life histories (Allen-Wardell et al. 1998). Managers of endangered plant species usually are unable to take community-level processes like pollination and seed dispersal into consideration because of this lack of basic biological information.

Global climate change is occurring (Bradley 2001) and will profoundly affect Earth's biota (Markham 1996; McCarty 2001; Pounds and Crump 1994; Wilson 2002), including rare species (Brown et al. 1997; Saetersdal and Birks 1997). The mechanisms underlying these effects will be complex, but one possibility for flowering plants is disruption of obligate pollination mutualisms (Spira 2001). For example, Harrison (2000) reported that pollination mutualisms between *Ficus* L. species and fig wasps in Borneo were seriously impacted by an extended drought associated with the 1997–1998 El Niño-Southern Oscillation (ENSO) event. Studies that have documented changes in plant phenology in response to global warming (e.g., Abu-Asab et al. 2001), in combination with others that have shown that plants and animals may respond to different climatic cues and thus their synchrony may be disrupted (e.g., Visser and Holleman 2001), indicate that asynchrony between plants and pollinators may be an indirect effect of global climate change.

Studies of climate change on organisms can take several approaches. Direct manipulation of a climatic parameter such as temperature (e.g., Price and Waser 1998) is an appealing approach, but Ringold and Groffman (1997) argue that the effects of climate change are too complex to be adequately modeled by simple manipulative studies. Schlesinger et al. (2001) suggested that studies of the response of ecosystems to inter-annual variation in climatic parameters could indicate how global climate change might impact them. In the context of rare plant population biology, studies of the pollination biology of rare plant species that include years with markedly varying climate can illustrate how rare species may be impacted by global climate change. Thus, multi-year pollination biology studies can provide valuable information to managers of rare plant populations.

Clematis socialis Kral (Ranunculaceae), was first described from Alabama in 1980 (Kral 1982) and soon was listed as federally endangered (U.S. Fish and Wildlife Service 1986). Initially known from only the type locality, *C. socialis* is now known from five sites in Alabama and Georgia and it is estimated that the species inhabits a total area of only ca. 0.4 ha (Boyd and Hilton 1994), and because it was only recently recognized, little is known about its reproductive biology. Timmerman-Erskine and Boyd (1999) found that naturally pollinated flowers were twice as likely to set fruit as flowers that were bagged before anthesis, showing that floral visitors were important for *C. socialis* fruit set. However, natural pollination services did not maximize fruit set, as supplemental hand pollination significantly increased fruit set 68% compared to naturally pollinated flowers (Timmerman-Erskine and Boyd 1999). Timmerman-Erskine and Boyd (1999) concluded that pollinator activity was less than optimum and limited fruit set by *C. socialis*. However, their study was not designed to identify pollinators of *C. socialis* and so, despite having demonstrated the importance of pollinators, their identities were still unknown. Thus, management of populations is still hampered by this lack of information on *C. socialis* mutualists.

The purpose of this study was to explore further the pollination biology of *C. socialis*. Our objectives were to: (1) identify the suite of floral visitors and determine the efficiency of the most prevalent visitors in pollinating *C. socialis*; (2) document the effect of interannual climate variation on the timing of flowering in *C. socialis;* and (3) consider how a change in floral phenology may influence the interaction of *C. socialis* with its pollinators.

METHODS

Study species

Clematis L., contains approximately 300 species worldwide of which 32 occur in North America (Pringle 1997a). Although most other members of the genus are vines, *C. socialis* is unusual, being an erect to trailing herbaceous perennial (Pringle 1997b). *Clematis socialis* also differs from most other members of its genus in that its achenes are not plumose and plants arise from horizontal patch-forming rhizomes (Pringle 1997b). Typical of most members of its family, *C. socialis* flowers have multiple stamens and multiple carpels. The carpels mature into an aggregate of single-seeded achenes.

Study site

This study was conducted at the Nature Conservancy's Dry Creek Preserve in St. Clair County, Alabama. This site contains the largest known population of *C. socialis*: approximately 14,000 stems, or 75% of known extant plants (Boyd and Hilton 1994). The site can be divided into two main subpopulations of plants that, although only 10–

15 m apart, occur in markedly different habitats. One subpopulation (hereafter termed the roadside subpopulation) of approximately 860 stems is located on the right-of-way of a U.S. highway 231 (Boyd and Hilton, 1994). The other subpopulation (hereafter called the woods subpopulation) of approximately 13,000 stems is located in a bottomland hardwood/pine community that was selectively logged in 1984 (Boyd and Hilton 1994).

Kral (1982) described the vegetation of the roadside subpopulation as a grass-sedge-rush community. Many herbaceous taxa co-occurred with *C. socialis* in this area, including *Gratiola floridana* Nutt., *Ranunculus* L. spp., and *Phlox glaberrima* L. (Kral 1982). Boyd and Hilton (1994) documented species associated with *C. socialis* in the more extensive woods subpopulation. *Phlox glaberrima*, *Coreopsis tripteris* L., *Duchesnea indica* (Andrz.) Focke, *Lonicera japonica* Thunb., and *Solidago* L. spp. are some of the more common plant species associated with *C. socialis* in this area. A more complete list of associated species in the woods subpopulation is available in Boyd and Hilton (1994).

Floral visitors and foraging behavior

Behavior of floral visitor species (time spent on and off of flowers during a foraging bout) was quantified to determine which visitors might be important in the pollination of *C. socialis*. Behavioral observations were recorded in the field using a hand-held tape recorder. Observations were made while walking along transects (see below) in the woods subpopulation or while walking through the roadside subpopulation. As soon as a potential floral visitor was seen, the recorder was started. Floral visitors were then followed and their activities were described into the tape recorder until they either left the site or were lost from view. Tapes describing visitor behavior were transcribed, and a stopwatch was used to quantify the time visitors spent "on" and "off" flowers during a foraging bout. These observations were used to calculate the floral visitation rate for each foraging bout observed, defined as number of flowers visited per minute of foraging time. Visitation rates for floral visitors were compared by Analysis of Variance (ANOVA), using Fisher's Protected Least Significant Difference (PLSD) test for post-hoc means comparisons (Abacus Concepts 1998). A few floral visitors were collected each year to confirm field identifications.

In both 1996 and 1997, observations of floral visitors were made several times during the flowering season (March–June). We observed floral visitors for approximately 24 and 32 h in 1996 and 1997, respectively. Although at least some observations were made during all daylight hours (0700 to 1900 h), the majority of the observations were made during the morning (0700 h) to midafternoon (1500 h) period, when insect activity was greatest. No observations of floral visitors were attempted between sunset and sunrise. Although quantitative data were not collected in 1994 and 1995, some qualitative remarks based on limited observations from these years are included.

Pollinator effectiveness

Pollinator effectiveness was measured using the "single visit" technique, which permits evaluation of the effectiveness of a floral visit to the plant and comparison of pollinator effectiveness among pollinator species (Motten et al. 1981). Flower buds nearing anthesis were covered with bags made of fine mesh bridal veil until buds opened. At that time, the bag was removed and the flower was observed until visited once. When the floral visitor departed, the stem was marked with a plastic bird band and pin flag. The flower was rebagged and remained bagged until achenes were full-sized and could be counted. Control flowers were treated similarly (bagged, unbagged, marked and rebagged) but were not visited by an insect while unbagged. On four occasions, twice in May 1996 and twice in April 1997, 16 to 20 flowers from the wooded population were used for the single visitor study by the above technique.

Achene production data were analyzed to determine if insect visitation significantly affected achene set and if single visit seed set differed between species of floral visitors. Data were analyzed by ANOVA, and Fisher's PLSD test was used for post-hoc means comparisons (Abacus Concepts 1998). Achene counts were square root transformed prior to analysis to meet the assumptions underlying ANOVA better (Zar 1996).

Seasonal timing of flower production

Data on the timing and extent of flower production were collected in each of four consecutive years. Starting at the beginning of the 1994, 1995, 1996 and 1997 flowering seasons, stems of *C. socialis* bearing an open flower were counted once a week until flowering ceased. The woods subpopulation was sampled using three belt transects (2 m wide by 30 m long) approximately 10 m apart. The total number of open flowers on all plants was recorded in the much smaller roadside subpopulation.

Temperature data were used to document climate differences between years. Monthly temperature data were obtained from the weather station at Talladega in Talladega County, Alabama (U.S. National Oceanic and Atmospheric Administration, 1994–1997). This station is located about 45 km SSE from the study site and by 1997 had collected 109 years of temperature data. We used temperature deviation from the 109-year mean, heating degree days (HDD), and cooling degree days (CDD) for the month of March in each year to judge if a particular season was relatively warm or cool. Menzel et al. (2001) reported that plant phenology in spring is usually linked more strongly to temperature than other climatic variables. Because *C. socialis* is a spring-flowering species that emerges from underground rhizomes in late February/ March, temperature values are good correlates of weather at the time of year in which plants are emerging and beginning to flower.

RESULTS

Floral visitors and foraging behavior

Five species of insects were recorded as visitors to *Clematis socialis* flowers: *Anthophora ursina* Cress. (Hymenoptera: Apidae), *Bombus pennsylvanicus* (DeGeer) (Hymenoptera: Apidae), *Xylocopa virginica* (L.) (Hymenoptera: Apidae), *Hemaris diffinis* (Bdv.) (Lepidoptera: Sphingidae) and *Erynnis juvenalis* (Fabricius) (Lepidoptera: Hesperiidae). Their abundance and behavior are described in the following sections and summarized in Table 1.

Anthophora ursina. Females of *Anthophora ursina* were responsible for 81% (N = 77) of the 94 observed visits to *C. socialis* flowers in 1996 but *A. ursina* was never observed visiting *C. socialis* in 1997. However, in 1997 *A. ursina* was observed visiting flowers of many other species in the woods subpopulation of our study site, particularly *Pedicularis canadensis* L. and *Sisyrinchium angustifolium* Miller. *Anthophora ursina* demonstrated high floral constancy in 1996. During the nine foraging bouts observed in that year, this species never switched to another floral host after foraging on *C. socialis* flowers. Females appeared to be foraging for both nectar and pollen. Several females were seen with large pollen loads on their hind legs. Males of this species were observed foraging at the site but never on *C. socialis*.

Bombus pennsylvanicus. Queens were observed visiting *C. socialis* flowers in both the woods and the roadside subpopulations during all four years of the study. During 1996, *B. pennsylvanicus* accounted for only 2% of the 94 visits observed. These visits, however, were restricted to the first week of the flowering season. In 1997, *B. pennsylvanicus* performed all of the 75 observed floral visits. During

Table 1. Summary of floral visitor behavior. Data are means (SD in parentheses). Differing superscripts for means within a column indicate means that differ significantly at ∝≤0.05 (Fisher's PLSD test). An asterisk in the column for 1997 indicates that this species was observed at the study site during that year, but was not observed visiting *C. socialis* flowers.

Floral visitor	Percentage of visits in 1996 (N = 94)	Percentage of visits in 1997 (N = 75)	Mean visitation rate (flowers/min)	Pollinator effectiveness (achenes/flower)
A. ursina	81.90%	0%*	9.1^{A} (4.2), N = 9	3.1^{A} (2.5), N = 7
B. pennsylvanicus	2.10%	100%	3.4^{B} (1.9), N = 13	2.6^{A} (2.0), N = 11
E. juvenalis	5.30%	0%	3.3^{B} (0.1), N = 2	n/a
H. diffinis	7.40%	0%*	7.4^{A} (1.5), N = 2	n/a
X. virginiana	3.20%	0%*	n/a	n/a

three of the 13 foraging bouts observed in 1997, individuals of *B. pennsylvanicus* were observed to switch floral hosts during a bout. Alternate hosts included *Amsonia tabernaemontana* Walter, *Carduus spinosissimus* Walter, and *Sisyrinchium angustifolium*. *Bombus pennsylvanicus* was never observed carrying visible pollen loads. Indeed, after visiting flowers of *C. socialis* a number of queens were observed grooming pollen off of their bodies.

Xylocopa virginiana. This carpenter bee robbed *C. socialis* flowers, obtaining nectar by piercing the base of the sepals and inserting its proboscis through the hole. Individuals of *X. virginiana* were never observed to make legitimate visits and thereby contact the reproductive parts of *C. socialis* flowers. *Xylocopa virginiana* was responsible for 3% of the 94 observed visits in 1996. Although present in 1997, *X. virginiana* was not observed visiting flowers of *C. socialis*. We were unable to collect visitation rates for *X. virginiana*, as individuals flew away after a single visit.

Hemaris diffinis. Commonly known as the snowberry clearwing, *H. diffinis* is a day-active sphingid moth whose coloration closely resembles that of a bumblebee. *Hemaris diffinis* typically hovered in front of flowers while probing them for nectar with its long proboscis. We observed this moth species visiting *C. socialis* flowers in both woods and roadside subpopulations during 1994, 1995 and 1996. During 1996, *H. diffinis* was responsible for 7% of the 94 observed visits to *C. socialis*. Although *H. diffinis* was observed at the study site in 1997, we did not record it visiting *C. socialis* flowers.

Erynnis juvenalis. The southern cloudy wing is a hesperiid butterfly. Typically, *E. juvenalis* would land on the outside of the sepals and probe a flower with its proboscis. We observed it visiting *C. socialis* flowers in the woods during the 1994 and 1996 seasons but did not see this species during the 1995 and 1997 seasons. During 1996, *E. juvenalis* was responsible for 5% of the 94 visits we observed.

Floral visitors differed significantly in their visitation frequency, defined as flowers visited/min (ANOVA: $F_{3,22} = 7.3$, $P = 0.001$). *Anthophora ursina* visited significantly more flowers per minute (almost 3-fold more) than either *B. pennsylvanicus* or *E. juvenalis*, but did not differ from the visitation rate of *H. diffinis* (at $P = 0.05$, Fisher's PLSD test, Table 1).

Pollinator effectiveness

Data on pollinator effectiveness were collected only for the two most common insect visitors, *A. ursina* and *B. pennsylvanicus*. During 1996, *A. ursina* was the only floral visitor abundant enough to allow us to conduct single-visit studies. In 1997, *B. pennsylvanicus* was the only observed floral visitor and thus was the only species available for use in single-visit studies. Pollinator visitation significantly increased achene set (ANOVA: $F_{3,37} = 32.4$, $P<0.0001$). Flowers visited by *A. ursina* set the most achenes (3.1 achenes/flower), followed closely at 2.6 achenes/flower set by flowers visited by *B. pennsylvanicus* (Table 1). Control flowers set very few achenes in both years. Mean achene set for control flowers in 1996 was 0.091 ± 0.30 (SD, N = 11) and in 1997 was 0.40 ± 1.0 (SD, N = 10). Fisher's PLSD test showed that bee-visited flowers set significantly more achenes than control flowers, but that achene set did not differ significantly between *A. ursina* and *B. pennyslvanicus* or between control treatments in 1996 and 1997 (at $P = 0.05$).

Seasonal timing of flower production

Over the four-year course of this study we observed a great deal of climatic variability for the month of March. Temperature deviated little from the 109-year mean in March 1994 (+0.28 °C) and March 1995 (+0.44 °C). Mean monthly temperature for March 1996 was strikingly below average, –2.0 °C (Fig. 1). On the other hand, mean monthly temperature for March 1997 was above average, +1.7 °C (Fig. 1). Values for heating degree-days and cooling degree-days for the month of March responded in relation to mean monthly temperature deviation (Fig. 1).

The flowering phenology of *C. socialis* was closely linked to the temperature patterns outlined above. Date of first flower of *C. socialis* is

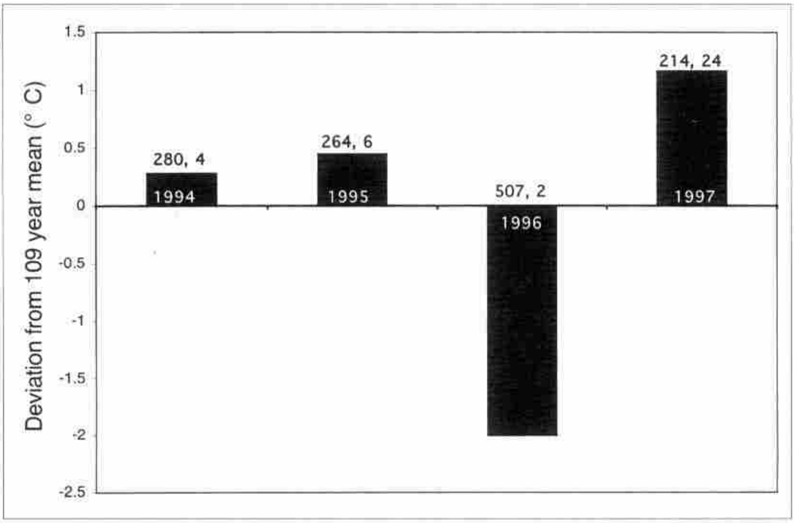

Figure 1. Deviation from mean monthly temperature (mean based on 109 year record) for March for 1994–1997. Number of heating degree days and cooling degree days for the month of March above each bar (HDD, CDD).

negatively correlated with deviation from monthly mean temperature ($r^2 = 0.86$) and CDD ($r^2 = 0.95$); and positively correlated with HDD ($r^2 = 0.82$). In both 1994 and 1995, the years in which temperatures deviated the least from average (Fig. 1), flowering peaked during the third week of April (Fig. 2). In 1996, a year of cooler than average temperatures (Fig. 1), peak flowering was delayed until the last week of April (Fig. 2). In contrast, during the warmest year of our study (1997; Fig. 1), peak flowering occurred during the first week of April (Fig. 2). Most importantly, there was only one week of overlap in the 1996 and 1997 flowering seasons of *C. socialis* (Fig. 2).

DISCUSSION

The five species of floral visitors we observed on *C. socialis* differ in their impact on its reproductive success. While Lepidoptera are clearly important pollinators for some species, they may function primarily as nectar thieves in plants with generalized floral morphologies (Adrienne et al. 1985, Lazri and Barrows 1984, Robertson 1924, Wiklund et al. 1979). In our study, both lepidopteran species were rarely recorded visiting flowers of *C. socialis*. Furthermore, when foraging at a flower, only the proboscis of the lepidopterans came into contact with the reproductive parts. Due to their low visitation frequency and the small surface area of their probosci available for pollen transfer, we do not expect either lepidopteran species to be a major contributor to pollination of *C. socialis*.

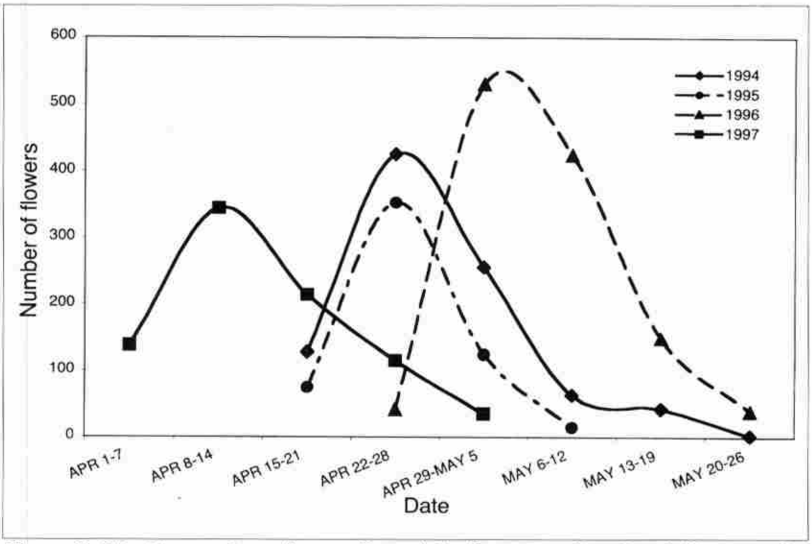

Figure 2. Weekly number of open *C. socialis* flowers at Dry Creek Preserve for four flowering seasons (1994–1997).

Bees were the other group of insect visitors to *C. socialis* flowers, but the three bee species observed in our study are not equally important to pollination. The nectar-robbing behavior of *X. virginiana* suggests that this species is more parasite than mutualist. We did not observe any behavior by this bee species that would directly result in pollen transfer between *C. socialis* flowers. However, despite the fact that nectar-robbing can have negative fitness effects on plants (e.g., Irwin and Brody 1999; Navarro 2001), it can also have neutral or even positive outcomes (Maloof and Inouye 2000; Navarro 2000). The net effect is dependent on the species-specific details of both the plant species and the floral visitors involved (Maloof and Inouye 2000), and further study of this phenomenon is needed to determine the net effect of *X. virginiana* on *C. socialis* pollination. However, because of its low prevalence on *C. socialis* flowers, we conclude that *X. virginiana* probably does not significantly affect pollination of *C. socialis*.

In contrast to *X. virginiana*, we conclude that the other two bee species are important pollinators of *C. socialis*. *Anthophora ursina* and *B. pennsylvanicus* were responsible for the vast majority of visits in at least one year and effected similar fruit set per visit (Table 1). But the mean visitation rate for *A. ursina* was ca. 3-fold greater than *B. pennsylvanicus* (Table 1). *Anthophora ursina* visited only *C. socialis* during its foraging bouts. Whereas, *B. pennsylvanicus* sometimes visited flowers of other species during foraging bouts and was often observed grooming pollen off its body, resulting in pollen wastage. This would make a strong case for focusing conservation priorities on *A. ursina* because it achieves more pollination per unit time. However, our data on inter-year variability in the flowering phenology of *C. socialis* should elicit caution for such a conclusion, and show the value of multi-year field studies.

Clematis socialis varied in flowering phenology during the four seasons of this study. The peak bloom of *C. socialis* usually occurs in mid-April, as we observed during 1994 and 1995 (Fig. 2). In 1996, however, unusually cool late winter temperatures in February and March delayed peak bloom until late April and early May. On the other hand, warmer conditions in March 1997 resulted in an earlier peak bloom (in early April 1997). Our study indicates that flowering in *C. socialis* is strongly influenced by average mean daily temperature in the winter resulting in either hastened flower production (if warm) or delayed flower production (if cool). This pattern is consistent with the conclusion of Menzel et al. (2001), that temperature is often the single most important climatic variable influencing springtime plant phenology.

In cases where flower production and pollinator emergence are not in phase, it is advantageous for the plant to host a suite of pollinators whose foraging times overlap with the potential flowering times of the plant. In this study, queens of *B. pennsylvanicus* pollinate *C. socialis* during early-season flowering. On the other hand, individuals of *A. ursina* do not begin to fly at our site until mid-April and thus are the principal pollinator of *C. socialis* during late-season flowering. While our data on visitation rates indicate that *A. ursina* is the most effective pollinator of *C. socialis*, this is not the most important result of our study. Instead, we show that management plans for *C. socialis* that focus exclusively on the most effective pollinator have the potential to fail to maintain sexual reproduction under variable climatic circumstances. Therefore, if a management plan that focuses on *A. ursina* and allows populations of *B. pennsylvanicus* to disappear is implemented, a series of "early" springs could seriously reduce sexual output in *C. socialis* by forcing the plant to rely upon a pollinator with a significantly lower floral visitation rate.

Global climate change will challenge humankind in many ways (Tilman and Lehman, 2001; Wilson, 2002), including serious conservation challenges (e.g., Brown et al., 1997; McCarty 2001; Saetersdal and Birks, 1997). Insect faunas may be seriously affected by climatic shifts (e.g., Kuchlein and Ellis 1997, Samways 1997) and the local extinction of pollinators is recognized as one threat to rare plant pollination mutualisms (Spira 2001). Our results show a different and more subtle way by which global climate change may impact pollination mutualisms of *C. socialis*. The very different temperature regimes of 1996 and 1997, and the different bee species that acted as pollinators in each year, show how a pollination mutualism can change if the climate of an area cools or warms. For *C. socialis*, if early springs predominate, then most pollination of *C. socialis* will be accomplished by *B. pennsylvanicus*. Late springs will favor pollination by *A. ursina*. Fortunately for *C. socialis*, both bee species have high single-visit seed set rates so that, despite the lower visitation rate of *B. pennsylvanicus* relative to *A. ursina*, at least some pollination can be accomplished regardless of how climate may change on our study site. Other plant species, which may rely on less effective pollinators, may experience more serious declines in pollinator service if climate change shifts their synchrony with pollinators. The threat of climate change to rare plants, through changing the synchrony of flowering and pollinator activity, should be added to the list of other factors (e.g., introduced pollinators, use of pesticides and herbicides, pollinator extinction, habitat loss) that can threaten pollination mutualisms of rare plants (Spira 2001).

It is becoming more widely accepted that pollinators must be considered in the management of endangered plant species (Allen-Wardell et al. 1998; Spira 2001). Classic examples of pollination (e.g., yucca moths, fig wasps, and orchid bees) give the false impression that all pollination systems are specialized (Waser et al. 1996). This idea is appealing to the resource manager with limited funds, as it suggests that management of a single important pollinator species will ensure adequate pollination. Our study indicates that design of management plans for rare plants must not only consider the ability of pollinators to impact the reproductive success of target species, but also how climatic and environmental variability will impact the success of those pollinators across time.

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